
Short Communication

Ixodid tick diversity on wild mammals, birds and reptiles in and around Etosha National Park, Namibia

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Introduction

There have been several surveys of the tick species that infest wildlife and domestic animals in various regions of Namibia. Horak *et al.* (1983) collected ticks from warthogs and from mountain zebras and horses (1984), Brain & Bohrmann (1992) examined baboons, Horak *et al.* (1992) sampled plains and mountain zebras, giraffes, kudus, gemsbok and springbok, Fourie, Horak & Woodall (2005) collected ticks from elephant shrews, Horak, Heyne & Donkin (2010) examined cheetahs, lions and a leopard and Pascucci *et al.* (2011) sampled African buffaloes. Biggs & Langenhoven (1984) and Nyangiwe *et al.* (2013) examined cattle and Matthee *et al.* (2010) dogs. A total of nineteen species of ixodid ticks were collected in these surveys, many of which infest both wild and domestic species.

The last tick survey in Etosha National Park (ENP) was conducted in the mid-1980s, and seven species of mammalian herbivores were examined, with seven tick species recovered (Horak *et al.*, 1992). In the present follow-up study, conducted from 2008–2010, we opportunistically sampled wild mammals, birds and reptiles in and around

ENP, Namibia, to determine the ticks present in the area and their host–parasite associations.

Material and methods

This study was conducted primarily in ENP, a 22,915 km² semi-arid savannah ecosystem in northern Namibia, located between 18°30'–19°30'S and 14°15'–17°10'E. Additional sampling occurred in other areas of Namibia, including Windpoort Farm, Lake Oponono, Swakopmund, Hardap National Park and from a roadkill along the B1 highway (Fig. 1). Sampling locations for each host species are provided in Table 1.

Plains zebra, black-backed jackal, African elephant and springbok were captured, sampled and many fitted with collars for other studies in ENP (sampling centred roughly around Okaukuejo camp: S 19.11988, E 15.91439) using methods detailed in Bellan *et al.* (2012), Cizauskas *et al.* (2014a,b) and Kamath *et al.* (2014). While animals were immobilized, they were examined for ticks (details below). Whenever possible, elephants, springbok and jackals, recaptured for collar removal, were re-sampled; recaptures of zebras were attempted every 6 months over 2–3 years, to sample in wet and dry seasons. Sampling of zebras took place from March 2008–August 2010, jackals from January 2009–June 2011, elephants from October 2008–July 2010 (sampling in dry seasons only) and springbok from August 2009–April 2010. Here, we present tick infestation data from 139 zebra immobilizations (from 68 unique individuals), 99 black-backed jackal immobilizations (96 unique individuals), 45 elephant immobilizations (33 unique individuals) and 13 springbok immobilizations (11 unique individuals).

Bird sampling was conducted by W.V. from June 2008–May 2009. Vulture chicks were sampled as part of an ongoing monitoring programme conducted by the Ministry of Environment and Tourism, where nests in ENP were monitored for breeding activity during the year. Vulture courtship commences in April; egg laying occurs between April and August (Brown *et al.*, 2015); and banding of chicks in the nest took place in September–November. These localities were scattered throughout ENP depending on

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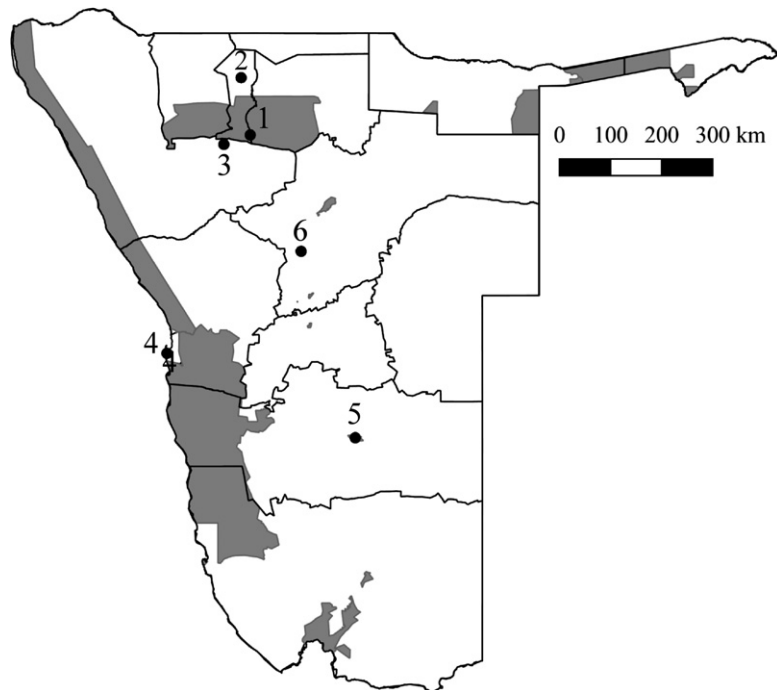


Fig 1 Sampling locations in northern and central Namibia. 1. Etosha National Park (the circle shows the location of Okaukuejo in central Etosha), 2. Lake Oponono, 3. Windpoort Farm, 4. Swakopmund, 5. Hardap National Park, 6. B1 Highway, located approximately 100 km north of Okahandja. Black lines indicate administrative regions of Namibia and grey polygons are government-protected areas

where the vultures nested and as the colonies moved. In addition, an adult Lappet-faced vulture was sampled as part of the study by Spiegel, Getz & Nathan (2013). All other birds were sampled by mist-netting. Standard mist-netting and bird-banding procedures and data reporting protocols were followed as specified by SAFRING, and ticks were collected while processing the bird.

Captured mammals (described above) were handled under IACUC R217-0509B (University of California, Berkeley), and captured birds under ringing licenses to W.V. from the Ministry of Environment and Tourism and SAFRING (No. 1119). All other sampled species were collected opportunistically, from road kills or animals captured, handled or destroyed by the staff of the Ministry of Environment and Tourism in the course of their duties.

Ticks were collected by examining each individual for approximately 2 min. The search areas varied by taxon: these included for mammals the ears, the tip of the tail, the thin skin at the base of the legs and around the groin and anus; for birds, the top of the head, around the ear opening and on the dorsal surface of the neck; and for reptiles, the ear and body scales (snakes) or the ear and nose (other reptiles). Upon collection, ticks were stored in 70% ethanol at room temperature. All specimens were identified by I.G.H. Estimates of prevalence were made only if two criteria were met: i) sampling records detailed

all animals thoroughly examined for ticks, including those with none found and ii) sample size was >5 host individuals.

Results and discussion

We examined 917 animals for ticks, consisting of 28 bird species ($N = 587$ individuals), 13 mammal species ($N = 322$ individuals) and six reptile species ($N = 8$ individuals) (Table 1). We recovered 981 ticks comprising a total of twelve species in the genera *Amblyomma*, *Hyalomma*, *Rhipicentor* and *Rhipicephalus* (Table 2).

Amblyomma exornatum

The 'leguan tick' infests monitor lizards in southern Africa, and the rock monitor and the water monitor are its preferred hosts (Horak *et al.*, 2006). *Amblyomma exornatum* has previously been documented in north and central Namibia, including ENP (Walker, 1991), and we recovered nymphs and adults from rock monitors in the park.

Amblyomma latum

The 'snake tick' infests several species of snakes, only incidentally other reptiles or mammals, and is widely

Table 1 Host species screened for ticks in Namibia and their sampling locations. Some locations are broadly defined, when the spatial extent of sampling was large (e.g. elephants were sampled throughout ENP); others are more specific, if the species was sampled at a single location. GPS coordinates for specific locations are Okaukuejo (S 19.17652, E 15.91736), Windpoort Farm (S 19.34143, E 15.45380), Lake Oponono (S 18.16886, E 15.75748), Swakopmund (S 23.01484, E 14.45340), Gemsbokvlakte (S 19.21870, E 16.05936) and Leeubron (S 19.07430, E 15.81057)

Scientific name	Common name	N sampled	N infested	Sampling location
Birds				
<i>Accipiter badius</i>	Little Banded Goshawk	1	1	Okaukuejo, ENP
<i>Amadina erythrocephala</i>	Red-headed Finch	6	0	Okaukuejo/Windpoort Farm
<i>Apus affinis</i>	Little Swift	7	0	Okaukuejo, ENP
<i>Charadrius pecuarius</i>	Kittlitz's Plover	17	0	Lake Oponono
<i>Cinnyris mariquensis</i>	Marico Sunbird	9	0	Okaukuejo, ENP
<i>Creatophora cinerea</i>	Wattled Starling	4	2	Okaukuejo, ENP
<i>Crithagra atrogularis</i>	Black-throated Canary	36	1	Okaukuejo, ENP
<i>Dicrurus adsimilis</i>	Fork-tailed Drongo	2	1	Okaukuejo, ENP
<i>Glaucidium perlatum</i>	Pearl-spotted Owlet	5	0	Okaukuejo, ENP
<i>Gyps africanus</i>	White-backed Vulture	18	0	central ENP
<i>Halcyon leucocephala</i>	Grey-headed Kingfisher	1	1	Okaukuejo, ENP
<i>Lamprotornis nitens</i>	Cape glossy Starling	48	6	Okaukuejo, ENP
<i>Melierax canorus</i>	Southern Pale Chanting Goshawk	2	1	Okaukuejo, ENP
<i>Monticola brevipes</i>	Short-toed Rock Thrush	5	0	Windpoort Farm
<i>Passer diffusus</i>	Southern Grey-headed Sparrow	30	0	Okaukuejo, ENP
<i>Philetairus socius</i>	Sociable Weaver	225	0	Okaukuejo, ENP
<i>Plocepasser mahali</i>	White-browed Sparrow-weaver	25	1	Okaukuejo/Windpoort Farm
<i>Ploceus intermedius</i>	Lesser Masked Weaver	7	0	Okaukuejo/Windpoort Farm
<i>Ploceus velatus</i>	Southern Masked Weaver	22	1	Okaukuejo/Windpoort Farm
<i>Pterocles bicinctus</i>	Double-banded Sandgrouse	5	0	Windpoort Farm
<i>Pycnonotus nigricans</i>	Red-eyed Bulbul	45	1	Okaukuejo/Windpoort Farm
<i>Pytilia melba</i>	Green-winged Pytilia	5	0	Okaukuejo/Windpoort Farm
<i>Quelea quelea</i>	Red-billed Quelea	27	0	Okaukuejo/Windpoort Farm
<i>Rhinoptilus africanus</i>	Double-banded Courser	7	0	central ENP/Windpoort Farm
<i>Spilopelia senegalensis</i>	Laughing Dove	7	0	Okaukuejo/Windpoort Farm
<i>Sterna hirundo</i>	Common Tern	8	0	Swakopmund
<i>Torgos tracheliotos</i>	Lappet-faced Vulture	9	1	central ENP
<i>Tricholaema leucomelas</i>	Pied Barbet	5	0	Okaukuejo/Windpoort Farm
Mammals				
<i>Diceros bicornis</i>	Black rhino	12	12	central-western ENP/Hardap NP
<i>Equus quagga</i>	Plains zebra	139	132	central ENP
<i>Giraffa camelopardalis</i>	Giraffe	2	2	central-eastern ENP
<i>Loxodonta africana</i>	African elephant	45	8	ENP
<i>Panthera leo</i>	Lion	3	3	central ENP
<i>Canis mesomelas</i>	Black-backed jackal	99	17	central ENP
<i>Antidorcas marsupialis</i>	Springbok	13	2	central ENP
<i>Hippotragus niger</i>	Sable antelope	1	1	Khoabendes, ENP
<i>Otocyon megalotis</i>	Bat-eared fox	1	1	Okaukuejo, ENP
<i>Crocuta crocuta</i>	Spotted hyaena	2	1	central ENP
<i>Mellivora capensis</i>	Honey badger	1	1	Gemsbokvlakte, ENP
<i>Xerus inauris</i>	Ground squirrel	3	3	central ENP
<i>Proteles cristata</i>	Aardwolf	1	1	B1 highway north of Okahandja
Reptiles				
<i>Boaedon capensis</i>	Brown house snake	1	1	Okaukuejo, ENP
<i>Naja nigricincta</i>	Zebra snake	1	1	Okaukuejo, ENP

(continued)

Table 1 (continued)

Scientific name	Common name	N sampled	N infested	Sampling location
<i>Naja</i> sp.	Cobra (subadult)	1	1	Okaukuejo, ENP
<i>Psammophis leopardalis</i>	Leopard sand snake	1	1	Okaukuejo, ENP
<i>Stigmochelys pardalis</i>	Leopard tortoise	1	1	Leeubron, ENP
<i>Varanus albigularis</i>	Rock monitor	3	3	central ENP

ENP = Etosha National Park.

distributed in the Afrotropical region (Walker, 1991; Horak *et al.*, 2006). It has previously been recorded in central Namibia around Okahandja and Gobabis (Walker, 1991). The present study expands its documented range to include ENP. We recovered a larva from a brown house snake, a nymph from a zebra snake and adults from a leopard sand snake and a subadult cobra.

Amblyomma marmoreum

The 'southern African tortoise tick' infests reptiles, most commonly tortoises, and has been recorded sporadically in the central and southern regions of Namibia (Walker, 1991). A single tick was recovered from a leopard tortoise in ENP, but demographic data for the tick were not recorded. This is the first record of *A. marmoreum* north of Outjo (Walker, 1991).

Hyalomma rufipes

The adults of *H. rufipes* infest a diversity of domestic and wild ungulates (Walker, 1991; Horak *et al.*, 1992; Espinaze *et al.*, 2016), while the immature stages commonly feed on birds and particularly on hares (Horak & Fourie, 1991; Van Niekerk, Fourie & Horak, 2006). We recovered adult *H. rufipes* from large mammalian herbivores, including plains zebras (11.5% prevalence), black rhinos and giraffe; nymphs from the Little Banded Goshawk, Wattled Starling, Black-throated Canary, Fork-tailed Drongo, Grey-headed Kingfisher, White-browed Sparrow-weaver (4.0% prevalence), Southern Masked Weaver (4.5% prevalence) and Red-eyed Bulbul (2.2% prevalence); and nymphs and larvae from Cape Glossy Starling (12.5% prevalence). With the exception of Red-eyed Bulbul, the other birds are new records for the immature stages of *H. rufipes* in southern Africa (Van Niekerk, Fourie & Horak, 2006; Hasle *et al.*, 2009). Including southern Africa, this tick is widely distributed

in the Afrotropical region (Apanaskevich & Horak, 2008a).

Hyalomma truncatum

Like *H. rufipes*, the adults of *H. truncatum* primarily infest wild and domestic ungulates, while the immature stages infest hares and murid rodents (Apanaskevich & Horak, 2008b). We recorded adult ticks on large mammals, including plains zebras (20.1% prevalence), black rhinos, African elephants, giraffe and lions. This is the first record of *H. truncatum* on African elephants, and 17.8% of elephants sampled in ENP were infested. In keeping with the host patterns documented in Apanaskevich & Horak (2008b), we recovered no immature stages from any of the 28 bird species examined. However, a single adult tick was collected from an adult Lappet-faced Vulture, which it likely acquired from feeding on an ungulate carcass. *Hyalomma truncatum* is widely distributed throughout Africa (Apanaskevich & Horak, 2008b).

Rhipicentor bicornis

Wild and domestic carnivores, including several species of canids, felids and genets are the preferred hosts of *R. bicornis* adults (Walker, 1991; Horak, Heyne & Donkin, 2010). Including northern Namibia, it is present from South Africa to central Africa (Walker, 1991). We collected a single adult tick from a lion in ENP.

Rhipicentor nuttalli

The adults of *R. nuttalli* infest hedgehogs, porcupines, leopards, other wild carnivores and domestic dogs and cats (Walker, 1991; Horak, Heyne & Donkin, 2010; Matthee *et al.*, 2010). This tick is distributed across southern and central Africa (Walker, 1991). We recovered a single adult tick on a black-backed jackal in central ENP, representing a prevalence of 1.0% on this host species.

Table 2 Tick infestations on Namibian wildlife. All specimens were collected in Etosha National Park unless otherwise noted

Tick–host associations	Host common name	Hosts infested/ sampled	Prev. (%)	Total number of ticks recovered				
				Larvae	Nymphs	Males	Females	Total
<i>Amblyomma exornatum</i>								
<i>Varanus albigularis</i>	Rock monitor	3/3	–	0	3	6	2	11
<i>Amblyomma latum</i>								
<i>Boaedon capensis</i>	Brown house snake	1/1	–	1	0	0	0	1
<i>Naja nigricincta</i>	Zebra snake	1/1	–	0	1	0	0	1
<i>Naja</i> sp.	Cobra (subadult)	1/1	–	0	0	1	1	2
<i>Psammophis leopardalis</i>	Leopard sand snake	1/1	–	0	0	1	1	2
<i>Amblyomma marmoreum</i>								
<i>Stigmochelys pardalis</i>	Leopard tortoise	1/1	–	–	–	–	–	1
<i>Hyalomma rufipes</i>								
<i>Diceros bicornis</i>	Black rhino	3/6	–	0	0	5	0	5
<i>Diceros bicornis</i> ^a	Black rhino	5/6	–	0	0	7	5	12
<i>Equus quagga</i> ^b	Plains zebra	16/139	11.5	0	0	12	5	17
<i>Giraffa camelopardalis</i>	Giraffe	2/2	–	0	0	2	0	2
<i>Accipiter badius</i>	Little Banded Goshawk	1/1	–	0	1	0	0	1
<i>Creatophora cinerea</i>	Wattled Starling	2/2	–	0	2	0	0	2
<i>Crithagra atrogularis</i>	Black-throated Canary	1/1	–	0	1	0	0	1
<i>Dicrurus adsimilis</i>	Fork-tailed Drongo	1/1	–	0	3	0	0	3
<i>Halcyon leucocephala</i>	Grey-headed Kingfisher	1/1	–	0	3	0	0	3
<i>Plocepasser mahali</i> ^c	White-browed Sparrow-weaver	1/25	4.0	0	1	0	0	1
<i>Ploceus velatus</i> ^c	Southern Masked Weaver	1/22	4.5	0	1	0	0	1
<i>Pycnonotus nigricans</i> ^c	Red-eyed Bulbul	1/45	2.2	0	1	0	0	1
<i>Lamprotornis nitens</i>	Cape Glossy Starling	6/48	12.5	2	6	0	0	8
<i>Hyalomma truncatum</i>								
<i>Diceros bicornis</i>	Black rhino	5/6	–	0	0	31	16	47
<i>Diceros bicornis</i> ^a	Black rhino	5/6	–	0	0	14	7	21
<i>Equus quagga</i> ^b	Plains zebra	28/139	20.1	0	0	41	17	58
<i>Giraffa camelopardalis</i>	Giraffe	2/2	–	0	0	55	20	75
<i>Loxodonta africana</i> ^b	African elephant	8/45	17.8	0	0	8	4	12
<i>Panthera leo</i>	Lion	2/3	–	0	0	4	1	5
<i>Torgos tracheliotus</i> ^d	Lappet-faced Vulture	1/9	–	0	0	1	0	1
<i>Rhipicentor bicornis</i>								
<i>Panthera leo</i>	Lion	1/3	–	0	0	1	0	1
<i>Rhipicentor nuttalli</i>								
<i>Canis mesomelas</i> ^b	Black-backed jackal	1/99	1.0	0	0	0	1	1
<i>Rhipicephalus evertsi mimeticus</i>								
<i>Equus quagga</i> ^b	Plains zebra	127/139	91.4	0	1	469	108	578
<i>Antidorcas marsupialis</i> ^b	Springbok	2/13	15.4	0	2	0	1	3
<i>Hippotragus niger</i>	Sable antelope	1/1	–	0	14	0	0	14
<i>Otocyon megalotis</i>	Bat-eared fox	1/1	–	0	4	0	0	4
<i>Rhipicephalus gertrudae</i>								
<i>Diceros bicornis</i> ^a	Black rhino	5/6	–	0	0	28	12	40
<i>Rhipicephalus sulcatus</i>								
<i>Equus quagga</i> ^b	Plains zebra	1/139	0.7	0	0	0	1	1
<i>Canis mesomelas</i> ^b	Black-backed jackal	11/99	11.1	0	0	13	4	17
<i>Crocuta crocuta</i>	Spotted hyaena	1/2	–	0	0	1	3	4

(continued)

Table 2 (continued)

Tick–host associations	Host common name	Hosts infested/ sampled	Prev. (%)	Total number of ticks recovered				
				Larvae	Nymphs	Males	Females	Total
<i>Rhipicephalus theileri</i>								
	<i>Mellivora capensis</i>	Honey badger	1/1	–	–	–	–	3
	<i>Xerus inauris</i>	Ground squirrel	3/3	–	0	1	0	2
<i>Rhipicephalus turanicus</i>								
	<i>Canis mesomelas</i> ^b	Black-backed jackal	7/99	7.1	0	0	8	2
	<i>Equus quagga</i> ^b	Plains zebra	1/139	0.7	0	0	0	1
	<i>Melierax canorus</i>	Southern Pale Chanting Goshawk	1/1	–	0	0	1	1
	<i>Otocyon megalotis</i>	Bat-eared fox	1/1	–	0	0	2	0
	<i>Panthera leo</i>	Lion	1/3	–	0	0	1	1
	<i>Proteles cristata</i> ^c	Aardwolf	1/1	–	0	0	0	1

^asampled in Hardap National Park, Namibia.

^bincludes some re-sampling of marked individuals, see Methods for details.

^cindividuals sampled were either from Okaukuejo in ENP or from Windpoort Farm located south of ENP.

^dinfested individual was an adult, all others sampled were chicks in the nest.

^eroadkill sampled on the B1 highway in the Otjozondjupa region of Namibia.

Rhipicephalus evertsi mimeticus

Various domestic and wild herbivores are hosts of *R. e. mimeticus* with most collections from equids and greater kudu (Horak, Biggs & Reinecke, 1984; Horak *et al.*, 1992; Walker, Keirans & Horak, 2000). *Rhipicephalus e. mimeticus* is present in the western region of south-central Africa from southern Namibia through Angola to the western tip of the Democratic Republic of the Congo, with introductions documented in South Africa (Walker, Keirans & Horak, 2000). We found this species primarily on plains zebra (91.4% prevalence), while several individuals were also collected from springbok (15.4% prevalence), a sable antelope and a bat-eared fox. Although nymphs were collected from all four host species, most ticks collected were adults on zebras. *Rhipicephalus e. mimeticus* has not previously been recorded on sable or bat-eared fox. The sable population in ENP has been introduced, and the natural distribution of sable does not overlap that of *R. e. mimeticus*.

Rhipicephalus gertrudae

Adults of this species tend to parasitize larger herbivores (Walker, 1991). However, several collections have been made from domestic dogs and some from domestic cats and caracals (Horak & Matthee, 2003; Horak, Heyne & Donkin, 2010; Matthee *et al.*, 2010). Walker *et al.* (2000) plot locality records across Namibia and south-central South

Africa. In the survey of several herbivore species conducted by Horak *et al.* (1992), *R. gertrudae* was not recovered from any of the hosts examined in ENP or Hardap National Park. We recovered adult ticks from five of six black rhinoceroses examined in the Hardap National Park, but not from animals in ENP (including black rhinos). This is the first recorded association between *R. gertrudae* and black rhino (Walker, Keirans & Horak, 2000).

Rhipicephalus sulcatus

We recorded adult ticks on black-backed jackal, spotted hyaena and plains zebra. Excluding the records on several nonspecific 'jackals' summarized in Walker, Keirans & Horak (2000), none of these species has previously been reported in association with this tick. We collected a single adult tick from a zebra representing 0.7% prevalence. Prevalence on black-backed jackals on the other hand was 11.1%. With the exception of the southern parts of Namibia and South Africa, this species has a wide distribution throughout sub-Saharan Africa (Walker, Keirans & Horak, 2000).

Rhipicephalus theileri

Yellow mongoose, meercat and Cape ground squirrel are the preferred hosts of *R. theileri*, and its distribution in southern Africa coincides with the distribution of these

small mammals (Walker, Keirans & Horak, 2000). We found a nymph and two adults on ground squirrels. We also found three ticks on a honey badger, a new host association, but no demographic information was recorded for these ticks.

Rhipicephalus turanicus s.l.

This species name is used for a tick which differs in taxonomic features depending on the continent or sub-continent in which it is collected and for which a specific identity has yet to be assigned to the southern African specimens (Guglielmono *et al.*, 2014). In sub-Saharan Africa, the preferred wild hosts include several meso- to large carnivores, hares and various ground-feeding birds (Walker, Keirans & Horak, 2000). We collected adult ticks from black-backed jackal (7.1% prevalence), and a single plains zebra (0.7% prevalence), lion, aardwolf, bat-eared fox and Southern Pale Chanting Goshawk. All these mammals have previously been reported in association with this tick; however, the Southern Pale Chanting Goshawk, on which we found two adult ticks, represents a new host association (Walker, Keirans & Horak, 2000; Van Niekerk, Fourie & Horak, 2006; Hasle *et al.*, 2009).

Conclusion

Twelve ixodid tick species were collected from mammals, birds and reptiles in central and northern Namibia. The numbers collected from individual animals were generally low and with some exceptions the prevalence of infestation low. The recorded infestation rates are well below those reported in other parts of southern Africa (e.g. Horak *et al.*, 2000), but are consistent with those previously reported in our study area (e.g. Horak *et al.*, 1992).

Acknowledgements

We thank the Ministry of Environmental and Tourism (MET) in Namibia for permission to conduct this research. We are grateful to Werner Kilian, Ortwin Aschenborn, Steve Bellan, Shayne Kötting, Carrie Cizauskas, Pauline Kamath, Birgit Kötting, Dudu Sibanda, Gabriel Shatumbu, Kerryn Carter and Orr Spiegel for assistance in collecting ticks. Funding was provided by NIH GM083863 (to Wayne Getz). Ivan Horak was funded by the University of Pretoria and the National Research Foundation of South Africa.

References

- APANASKEVICH, D.A. & HORAK, I.G. (2008a) The genus *Hyalomma* Koch, 1844: V. re-evaluation of the taxonomic rank of taxa comprising the *H. (Euhyalomma) marginatum* Koch complex of species (Acari: Ixodidae) with redescription of all parasitic stages and notes on biology. *Int. J. Acarol.* **34**, 13–42.
- APANASKEVICH, D.A. & HORAK, I.G. (2008b) The genus *Hyalomma*. VI. Systematics of *H. (Euhyalomma) truncatum* and the closely related species, *H. (E.) albiparmatum* and *H. (E.) nitidum* (Acari: Ixodidae). *Exp. Appl. Acarol.* **44**, 115–136.
- BELLAN, S.E., CIZAUSKAS, C.A., MIYEN, J., EBERSOHN, K., KÜSTERS, M., PRAGER, K.C., VAN VUUREN, M., SABETA, C. & GETZ, W.M. (2012) Blacked-back jackal exposure to rabies virus, canine distemper virus and *Bacillus anthracis* in Etosha National Park. *Namibia. J. Wildl. Dis.* **48**, 371–381.
- BIGGS, H.C. & LANGENHOVEN, J.W. (1984) Seasonal prevalence of ixodid ticks on cattle in the Windhoek District of South West Africa/Namibia. *Onderstepoort J. Vet. Res.* **51**, 175–182.
- BRAIN, C. & BOHRMANN, R. (1992) Tick infestation of baboons (*Papio ursinus*) in the Namib Desert. *J. Wildl. Dis.* **28**, 188–191.
- BROWN, C., BRIDGEFORD, P., BRAINE, S., PAXTON, M. & VERSVELD, W. (2015) Breeding data on the birds of Namibia: laying months, colony and clutch sizes and egg measurements. *Ornithological Observations*. **6**, 92–196.
- CIZAUSKAS, C. A., BELLAN, S. E., TURNER, W. C., VANCE, R. E. & GETZ, W. M. (2014a) Frequent and seasonally variable sublethal anthrax infections are accompanied by short-lived immunity in an endemic system. *J. Anim. Ecol.* **83**, 1078–1090.
- CIZAUSKAS, C.A., TURNER, W.C., WAGNER, B., KÜSTERS, M., VANCE, R.E. & GETZ, W.M. (2014b) Gastrointestinal helminths may affect host susceptibility to anthrax through seasonal immune trade-offs. *BMC Ecol.* **14**, 27.
- ESPINAZE, M. P. A., HELLARD, E., HORAK, I. G. & CUMMING, G. S. (2016) Analysis of large new South African dataset using two host-specificity indices shows generalism in both adult and larval ticks of mammals. *Parasitol.* **143**, 366–373.
- FOURIE, L.J., HORAK, I.G. & WOODALL, P.F. (2005) Elephant shrews as hosts of immature ixodid ticks. *Onderstepoort J. Vet. Res.* **72**, 293–301.
- GUGLIELMONO, A.A., ROBBINS, R.G., APANASKEVICH, D.A., PETNEY, T.N., ESTRADA-PEÑA, A. & HORAK, I.G. (2014) *The Hard Ticks of the World (Acari: Ixodida: Ixodidae)*. Springer, Dordrecht, Heidelberg.
- HASLE, G., HORAK, I.G., GRIEVE, G., LEINAAS, H.P. & CLARKE, F. (2009) Ticks collected from birds in the northern provinces of South Africa, 2004–2006. *Onderstepoort J. Vet. Res.* **76**, 167–175.
- HORAK, I.G., BIGGS, H.C. & REINECKE, R.K. (1984) Arthropod parasites of Hartmann's mountain zebra, *Equus zebra hartmannae*, in South West Africa/Namibia. *Onderstepoort J. Vet. Res.* **51**, 183–187.
- HORAK, I.G. & FOURIE, L.J. (1991) Parasites of domestic and wild animals in South Africa. XXIX. Ixodid ticks on hares in the Cape Province and on hares and red rock rabbits in the Orange Free State. *Onderstepoort J. Vet. Res.* **58**, 261–270.

- HORAK, I. G., HEYNE, H. & DONKIN, E. F. (2010) Parasites of domestic and wild animals in South Africa XLVIII. Ticks (Acari: Ixodidae) infesting domestic cats and wild felids in southern Africa. *Onderstepoort J. Vet. Res.*, **77**, 1–7. Art. #3.
- HORAK, I.G. & MATTHEE, S. (2003) Parasites of domestic and wild animals in South Africa. XLIII. Ixodid ticks of domestic dogs and cats in the Western Cape Province. *Onderstepoort J. Vet. Res.* **70**, 187–195.
- HORAK, I.G., BIGGS, H.C., HANSEN, T.S. & HANSEN, R.E. (1983) The prevalence of helminth and arthropod parasites of warthog, *Phacochoerus aethiopicus*, in South West Africa/Namibia. *Onderstepoort J. Vet. Res.* **50**, 145–148.
- HORAK, I.G., ANTHONISSEN, M., KRECEK, R.C. & BOOMKER, J. (1992) Arthropod parasites of springbok, gemsbok, kudus, giraffes and Burchell's and Hartmann's zebras in the Etosha and Hardap Nature Reserves Namibia. *Onderstepoort J. Vet. Res.* **59**, 253–257.
- HORAK, I.G., BRAACK, L.E.O., FOURIE, L.J. & WALKER, J.B. (2000) Parasites of domestic and wild animals in South Africa. XXXVIII. Ixodid ticks collected from 23 wild carnivore species. *Onderstepoort J. Vet. Res.* **67**, 239–250.
- HORAK, I.G., MCKAY, I.J., HENEN, B.T., HEYNE, H., HOFMEYER, M.D. & DE VILLIERS, A.L. (2006) Parasites of domestic and wild animals in South Africa. XLVII. Ticks of tortoises and other reptiles. *Onderstepoort J. Vet. Res.* **73**, 215–227.
- KAMATH, P. L., TURNER, W. C., KÜSTERS, M. & GETZ, W. M. (2014) Parasite-mediated selection drives an immunogenetic trade-off in plains zebras (*Equus quagga*). *Proc Biol Sci.* **281**, 20140077.
- MATTHEE, S., LOVELY, C., GAUGLER, A., BEEKER, R., VENTER, H.R. & HORAK, I.G. (2010) Ixodid ticks on domestic dogs in the Northern Cape Province of South Africa and in Namibia. *J. S. Afr. Vet. Assoc.* **81**, 126–128.
- NYANGIWE, N., MATTHEE, C., HORAK, I. & MATTHEE, S. (2013) First record of the pantropical blue tick *Rhipicephalus microplus* in Namibia. *Exp. Appl. Acarol.* **61**, 503–507.
- PASCUCCI, I., DONDONA, A.C., CAMMÀ, C., MARCACCI, M., DI DOMENICO, M., LELLI, R., SCACCHIA, M., JAGO, M., KHAISEB, S., HAGER, A.L., TJIPURA-ZAIRE, G. & CAPORALE, V. (2011) Survey of Ixodid ticks and two tick-borne pathogens in African buffaloes, *Syncerus caffer*, from the Caprivi Strip, Namibia. *J. Zoo Wildl. Med.* **42**, 634–640.
- SPIEGEL, O., GETZ, W.M. & NATHAN, R. (2013) Factors influencing foraging search efficiency: why do scarce Lappet-Faced Vultures outperform ubiquitous White-Backed Vultures? *Am. Nat.* **181**, E102–E115.
- VAN NIEKERK, D.J., FOURIE, L.J. & HORAK, I.G. (2006) Birds as hosts of immature ixodid ticks in Free State Province, South Africa. *Onderstepoort J. Vet. Res.* **73**, 123–130.
- WALKER, J.B. (1991) A review of the Ixodid ticks (Acari, Ixodidae) occurring in southern Africa. *Onderstepoort J. Vet. Res.* **58**, 81–105.
- WALKER, J.B., KEIRANS, J.E. & HORAK, I.G. (2000) *The Genus Rhipicephalus (Acari, Ixodidae): A Guide to the Brown Ticks of the World*. Cambridge University Press, Cambridge, UK.

(Manuscript accepted 17 August 2016)

doi: 10.1111/aje.12369